Evidence for Reduction of Native Mosquitoes With Increased Expansion of Invasive *Ochlerotatus japonicus japonicus* (Diptera: Culicidae) in the Northeastern United States

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ABSTRACT *Ochlerotatus japonicus japonicus* (Theobald) is an invasive mosquito native to Japan, Korea, and eastern China. The species was first detected in the northeastern United States in 1998 and has rapidly spread throughout much of eastern North America. In addition to used tire casings, *Oc. j. japonicus* develops in a wide variety of artificial and natural container habitats, especially rock pools along stream beds. In an effort to evaluate the invasion success and impact of *Oc. j. japonicus* on populations of native container dwelling species, waste tire disposal sites and natural rock pool habitats were sampled for mosquito larvae throughout Connecticut in 2005, and data were compared with results from prior surveys made in 1987 and 1999. *Oc. j. japonicus* was the predominant species collected at the waste tire disposal sites regardless of surrounding landscape features, accounting for 55.9% of all larvae. A comparison with collections from prior surveys revealed a 90% reduction in the relative abundance of larval populations of *Oc. triseriatus* (Say) and significant reductions among larval populations of *Oc. atropalpus* (Coquillett) and *Culex restuans* Theobald. *Oc. j. japonicus* was also the most abundant mosquito collected in rock pool habitats, accounting for nearly 80% of all collected larvae, except where water temperatures exceeded 30°C. This was concomitant with significant declines in the relative abundance of *Oc. atropalpus* and *Cx. restuans*. We conclude that *Oc. j. japonicus* is a potentially effective competitor in rock pool and tire environments and may be responsible for reducing populations of several native species occupying these habitats through interspecific competition for limited resources. The exclusion of *Oc. j. japonicus* from warm water pools further suggests that a temperature barrier may exist for *Oc. j. japonicus* and that populations may not be able to colonize southern regions of the United States with relatively high summer temperatures.

KEY WORDS *Ochlerotatus japonicus japonicus*, interspecific competition, rock pools, tires, *Ochlerotatus atropalpus*

Ochlerotatus japonicus japonicus (Theobald) (=*Aedes japonicus japonicus*, see Reinert 2000) is an invasive mosquito native to Japan, Korea, and eastern China (Tanaka et al. 1979). The species was first detected in the northeastern United States (Connecticut, New Jersey, and New York) in 1998, and was likely introduced via importation of infested automobile tires (Peyton et al. 1999, Andreadis et al. 2001). In addition to used tire casings, *Oc. j. japonicus* develops in a wide variety of artificial and natural container habitats, especially rock pools along stream beds (Tanaka et al. 1979). *Oc. j. japonicus* produces freeze- and desiccation-resistant eggs that tolerate a broad range of temperature extremes and appears to be a rapid and efficient colonizing species in both rural and urban locales. To date, established populations have been

detected in at least 27 other states and two Canadian provinces (Ontario and Quebec) mostly in eastern North America (Morris et al. 2007).

Since the discovery of *Oc. j. japonicus* in North America, the majority of studies have largely focused on surveys of water-filled container habitats in different geographic regions to ascertain its establishment, distribution, and relative abundance (Andreadis et al. 2001, Sardelis and Turell 2001, Scott et al. 2001, Falco et al. 2002, Harrison et al. 2002, Oliver et al. 2003, Joy 2004, Reeves and Korecki 2004, Roppo et al. 2004, Young et al. 2004, Caldwell et al. 2005, Gallitano et al. 2005, Gray et al. 2005, Kaufman et al. 2005, Larish and Savage 2005, Sames and Pehling 2005, Holman et al. 2006, Saenz et al. 2006, Thielman and Hunter 2006, Morris et al. 2007, Hughes et al. 2008). Expanded investigations in selected regions of the United States with established populations have subsequently revealed increased abundance relative to other container-inhabiting species such as *Oc. triseriatus* (Say) (=*Ae. triseriatus*, see Reinert 2000)

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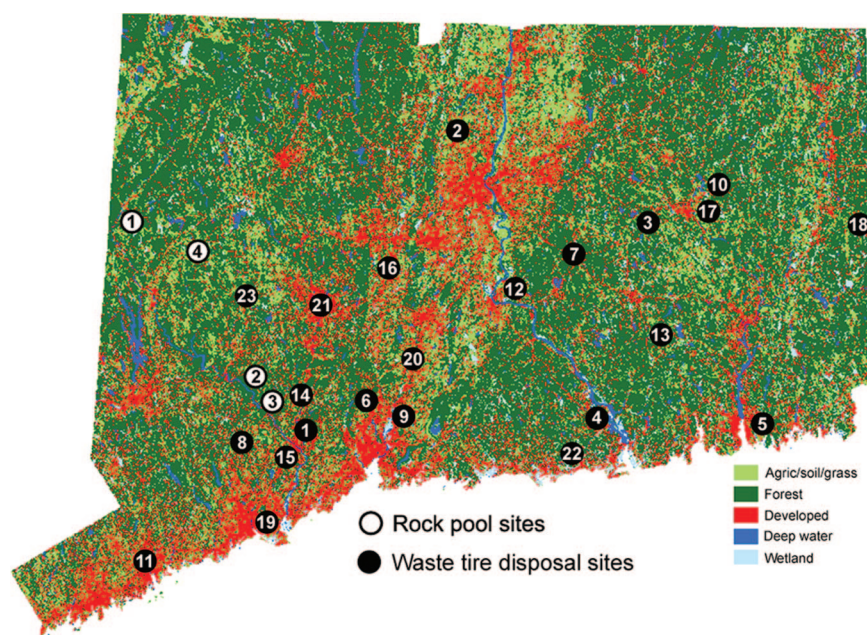
Fig. 1. Land use map of Connecticut showing the distribution of 23 waste tire disposal and four rock pool sample sites from which mosquito larvae were collected for comparative analysis in 1987, 1999, and 2005. (Online figure in color.)

and *Oc. atropalpus* (Coquillett) (=*Ae. atropalpus*, see Reinert 2000) (Joy and Sullivan 2005, Bevins 2007). These observations, in concert with its rapidly expanding distribution, suggest that *Oc. j. japonicus* may become a dominant invader capable of competitively reducing or displacing cohabiting species in certain habitats (Joy and Sullivan 2005, Juliano and Lounibos 2005, Bevins 2007, Lounibos 2007).

Oc. j. japonicus is well established in Connecticut and based on statewide surveys of natural rock pool and used tire habitats before and after its initial detection (Andreadis 1988, Andreadis et al. 2001), is generally thought to have colonized the region sometime between 1992 and 1998. During the last survey conducted in 1999 (Andreadis et al. 2001), *Oc. j. japonicus* was found to be moderately abundant in used tire casings, ranking fourth in overall abundance (9%) among eight other cohabitating species, and was the most commonly encountered species in rock pool habitats representing slightly >50% of all collected larvae (five cohabiting species). In an effort to evaluate the invasion success and impact of *Oc. j. japonicus* on other container dwelling species, we have continued to monitor larval populations in these specialized habitats. The results of our current investigation are reported herein in which we now provide evidence for increased relative abundance of *Oc. j. japonicus* throughout the region concomitant with declines in the relative abundance of native species.

Materials and Methods

Waste Tire Disposal Sites. Thirteen waste tire disposal sites throughout the state of Connecticut (Fig. 1) were sampled for larval mosquitoes in 2005 (site no. 1, 7, 10, 11, 14, 15, 16, 17, 18, 19, 21, 22, 23), and data were compared with results from previous statewide surveys of similar sites conducted in 1987 ($n = 9$; site no. 3, 5, 6, 8, 12, 13, 16, 19, 20) (Andreadis 1988), and 1999 ($n = 8$; site no. 2, 4, 5, 9, 12, 16, 18, 22) (Andreadis et al. 2001). Collection sites included waste tire piles from 19 disposal facilities and commercial tire dealerships, and four farms located in a variety of urban, suburban, and rural environments. The comparative proportion of developed (urban/suburban) and forest (rural/residential) land cover was additionally determined for collection sites using 2006 land use cover classification data from each respective municipality in which the waste tire disposal site was located. Land use data were obtained from the University of Connecticut Center for Land Use Education and Research (CLEAR 2009) where "developed" was defined as "high-density built-up areas associated with commercial, industrial and residential activities and transportation routes," and "forested" defined as "mixed deciduous and coniferous forests, and scrub areas characterized by patches of dense woody vegetation."

For the 2005 survey, each of the 13 sites was sampled every other week from April through October and once in early November ($n = 11$). On each collection date, the water contents from an average of 50 different tire casings were removed with a flexible 250 ml plastic cup. Efforts were made to collect samples from tires scattered throughout the site including those exposed to direct sunlight and those shaded by trees or low-lying vegetation. However, no attempt was made to separate and enumerate larvae from individual tires. Samples were transported to the laboratory

Table 1. Number of larval mosquitoes collected from used tires at 13 sites in Connecticut sampled from April to Nov. 2005

Municipality (site no.)	An. punctipennis	Cx. pipiens	Cx. restuans	Cx. territans	Oc. atropalpus	Oc. j. japonicus	Oc. triseriatus	Total
Ansonia (1)	5	—	47	2	—	268	2	324
Marlborough (7)	10	—	297	2	5	458	10	782
North Windham (10)	5	70	86	—	10	173	81	425
Norwalk (11)	—	241	53	—	3	292	139	728
Seymour (14)	8	9	79	—	—	575	3	674
Shelton (15)	1	26	132	4	—	205	—	368
Southington (16)	15	71	181	—	18	341	2	628
South Windham (17)	9	—	129	—	2	362	14	516
Sterling (18)	1	3	11	—	48	220	31	314
Stratford (19)	—	47	74	—	53	186	223	583
Waterbury (21)	10	47	1	—	2	491	8	559
Westbrook (22)	—	4	24	2	—	156	1	187
Woodbury (23)	2	398	284	2	—	133	—	819
Total	66	916	1,398	12	141	3,860	514	6,907

the following day and mosquito larvae were sorted, counted, and identified with the aid of a stereo microscope (90×) based on morphological characters and descriptive keys (Andreadis et al. 2005, Darsie and Ward 2005). Early instar larvae not readily identifiable were reared in 100 ml culture dishes at 27°C and identified as second to fourth instars. All mosquitoes were counted and identified to the species level. The relationships between the proportions of *Oc. j. japonicus* collected and the proportion of developed (urban/suburban) and forest (rural/residential) land cover for each collection site were analyzed by regression analyses (SPSS 2003). Collection data from all 13 sites were combined for comparative analysis with data from 1987 and 1999.

The collection and identification procedures used in 1987 and 1999 have been described previously (Andreadis 1988, Andreadis et al. 2001) and were largely the same except: the number of sampling dates at each site were more variable (1987 range 1–9, mean = 5 collection dates/site, n = 935 larvae) (1999 range 1–7, mean = 3 collection dates/site, n = 2,347 larvae) and did not include sampling in April and May (both years) or November (1987). Comparisons and analysis with the current 2005 survey therefore only included collection data from the same time period (June through October, n = 5,415 larvae), and data from all collection sites for each year were similarly pooled. Data were analyzed by χ^2 analysis using Yates's correction for continuity (SPSS 2003).

Rock Pool Sites. Four rock pool sites located along the Housatonic (site no. 1–3) and Shepaug (site no. 4) rivers were sampled for mosquito larvae in 2005 (Fig. 1). The number of individual pools sampled at each site, frequency and duration of sampling was as follows: Site no. 1 (Kent), 19 pools, once a week from mid-April through mid-November (n = 25 collection dates); site no. 2 (Oxford), 15 pools, once a week from late-April through mid-November (n = 24); site no. 3 (Seymour), 15 pools, once a week from mid-June through the end of September (n = 9); and site no. 4 (Washington), 15 pools once every other week from mid-May through the end of September (n = 9). Mosquitoes were collected with a long-handled 300-ml dipper and representative samples were taken from a variety of different pools at each site

that contained varying amounts of leaf litter, algae, and organic detritus. Individual pools ranged from 20 cm to 2.3 m in diameter (mean = 75 cm), and 10.2 cm to 1.3 m in depth (mean = 35.2 cm). Water temperature was additionally recorded with a handheld thermometer at midday from every pool at sites no. 1 and 2 on each sampling date. All mosquitoes were counted and identified to species as described above. Weekly collection data from various individual pools sampled at each site were combined for analyses for each collection date.

The relative abundance of mosquito species collected at Kent (site no. 1) in 2005 was contrasted with abundance data obtained from a prior survey of pools made at the same collection site in 1999 (Andreadis et al. 2001) wherein collections were made every 1–2 wk from July through November (n = 11 collection dates). Collection data obtained from the same time period (July to November) in 1999 and 2005 were analyzed by χ^2 analysis using Yates's correction for continuity (SPSS 2003).

Results

Waste Tire Disposal Sites. A total of 6,907 mosquito larvae were collected from the 13 waste tire disposal sites sampled from April through November of 2005 (Table 1). Seven mosquito species were identified among which *Oc. j. japonicus* was the most abundant, representing 55.9% of the total collection. Other species ranked in order of relative abundance included: *Culex restuans* (Theobald) (20.2%), *Cx. pipiens* (L.) (13.3%), *Oc. triseriatus* (7.4%), *Oc. atropalpus* (2.0%), *Anopheles punctipennis* (Say) (1.0%), and *Cx. territans* (Walker) (0.2%). *Oc. j. japonicus* was collected at all 13 sites and was the predominant species found at every site except Stratford (no. 19), a densely populated urban locale, and Woodbury (no. 23), a farm in a rural setting. *Oc. triseriatus* was slightly more abundant at Stratford (38.2 versus 32.0%), and both *Cx. pipiens* and *Cx. restuans* were more abundant at Woodbury (48.6 and 34.7%, respectively, versus 16.2%). The overall prevalence of *Oc. j. japonicus* at each of the 13 sites ranged from 87.8 to 16.2% (median = 58.6%, mean = 59.8%) and no significant associations were found between the proportion of *Oc. j. japonicus* col-
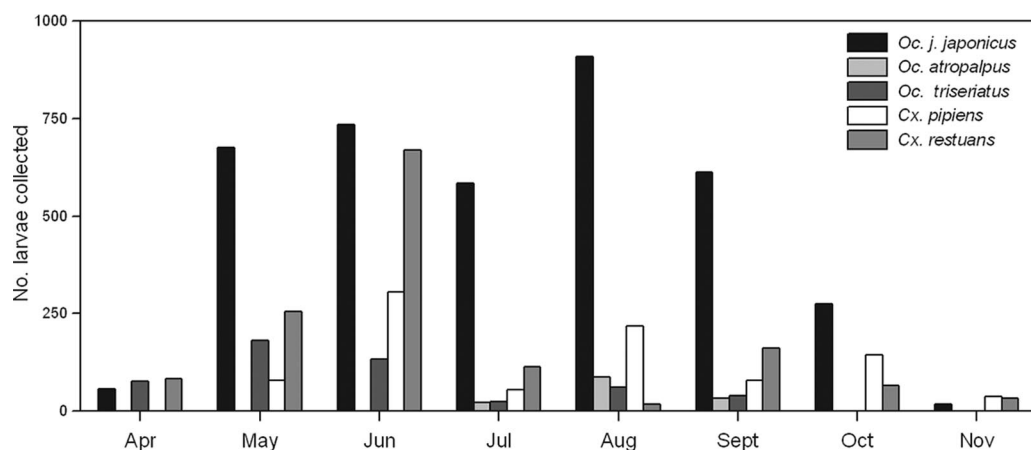
Fig. 2. Total monthly number of *Oc. j. japonicus*, *Oc. atropalpus*, *Oc. triseriatus*, *Cx. pipiens*, and *Cx. restuans* larvae collected from used tires at thirteen sites in Connecticut sampled from April to November 2005.

lected and the proportion of developed ($\hat{y} = 58.6 + 0.04\,x$, $r = 0.03$, $P = 0.92$) or forest ($\hat{y} = 53.8 + 0.12\,x$, $r = 0.11$, $P = 0.72$) land cover at each collection site.

Oc. j. japonicus was collected throughout the entire sampling period and with the exception of April and November, when comparatively few larvae were collected, was the most abundant species found each month (Fig. 2). *Oc. j. japonicus* was most abundant in August, representing nearly 70% of all species collected, and only during the month of June were equal numbers of another species (*Cx. restuans*) recorded (36.2 versus 39.7%). *Cx. restuans* was also the only other species that was collected each month. *Oc. triseriatus* was found from April through September, while *Oc. atropalpus* was limited to the warmer months of July, August, and September. *Cx. pipiens* was collected from May through October and like *Cx. restuans*, was most common in June.

An analysis of the relative abundance and composition of mosquito species collected from the waste tire disposal sites in 2005 ($n = 5,415$) with 1999 ($n = 2,347$) during the same time period (June to October) (Fig. 3), revealed a significantly greater proportion of *Oc. j. japonicus* in 2005 than in 1999 when the species was first detected (57.5 versus 9.2%, $\chi^2 = 1,555.4$, df = 1, $P < 0.001$). This was coincident with a significant decline in the proportion of *Oc. triseriatus* (44.5 versus 4.7%, $\chi^2 = 1,850.2$, df = 1, $P < 0.001$), which was the most frequently collected species in 1999. The proportion of *Oc. atropalpus* remained unchanged (2.6 versus 2.0%, $\chi^2 = 1.9$, df = 1, $P = 0.166$) but was significantly lower than that observed before the discovery of *Oc. j. japonicus* in 1987 ($n = 935$) (19.3%, $\chi^2 = 456.9$, df = 1, $P < 0.001$). These changes in proportional abundance were also reflected in corresponding increases or declines in the absolute number of larvae collected for each species (Table 2).

The relative abundance of *Cx. restuans* observed in 2005 was significantly less than in 1999 (19.0 versus 32.5%, $\chi^2 = 168.0$, df = 1, $P < 0.001$) and 1987 (27.8%, $\chi^2 = 37.8$, df = 1, $P < 0.001$). *Cx. pipiens* by contrast,

was significantly more abundant in 2005 than in 1999 (14.8 versus 9.3%, $\chi^2 = 42.8$, df = 1, $P < 0.001$), but its abundance was no different than that observed in 1987 (17.1%, $\chi^2 = 3.2$, df = 1, $P = 0.073$).

Although infrequently found, *An. punctipennis* was the only native species that was significantly more abundant in 2005 than in 1999 (1.2 versus 0.2%, $\chi^2 = 17.2$, df = 1, $P < 0.001$), but its prevalence in 2005 was significantly less than in 1987 where it accounted for 4.2% of the total collection ($\chi^2 = 43.6$, df = 1, $P < 0.001$).

Rock Pool Sites. *Oc. j. japonicus* was detected from April through November and was the most abundant species found at three of four collection sites representing 78.4% (Kent, $n = 14,594$), 81.0% (Washington, $n = 332$), and 95.7% (Seymour, $n = 374$) of all species collected (Fig. 4). The only location where *Oc. j. japonicus* did not dominate was the collection site along the lower regions of the Housatonic River in Oxford where a preponderance of *Oc. atropalpus* larvae were found, most notably during the warmer months of June through September, accounting for 77.6% ($n = 585$) of all species in comparison to 13.2% for *Oc. j. japonicus.* An analysis of monthly mean water temperatures recorded at midday in the rock pools from the Oxford site revealed temperatures $\geq 32°C$ during this time period (May 16.0, June 33.0, July 32.0, August 32.0, September 32.2, October 16.0, November 18.0°C). This was notably higher than the temperatures recorded among water-filled pools along the upper regions of the Housatonic River at the site in Kent (May 12.8, June 21.8, July 22.8, August 23.8, September 17.7, October 7.8, November 10.9°C). *Oc. atropalpus* was additionally collected at the Kent and Seymour sites but was considerably less abundant accounting for 8.4 and 0.8%, respectively. Other species collected included *Cx. restuans* (two sites, 5.7%), *An. punctipennis* (four sites, 4.3%), *Cx. territans* (two sites, 2.0%), and *Cx. pipiens* (one site, 1.0%).

Analysis of collection data on the abundance and composition of mosquito species collected from rock pools along the upper portions of the Housatonic
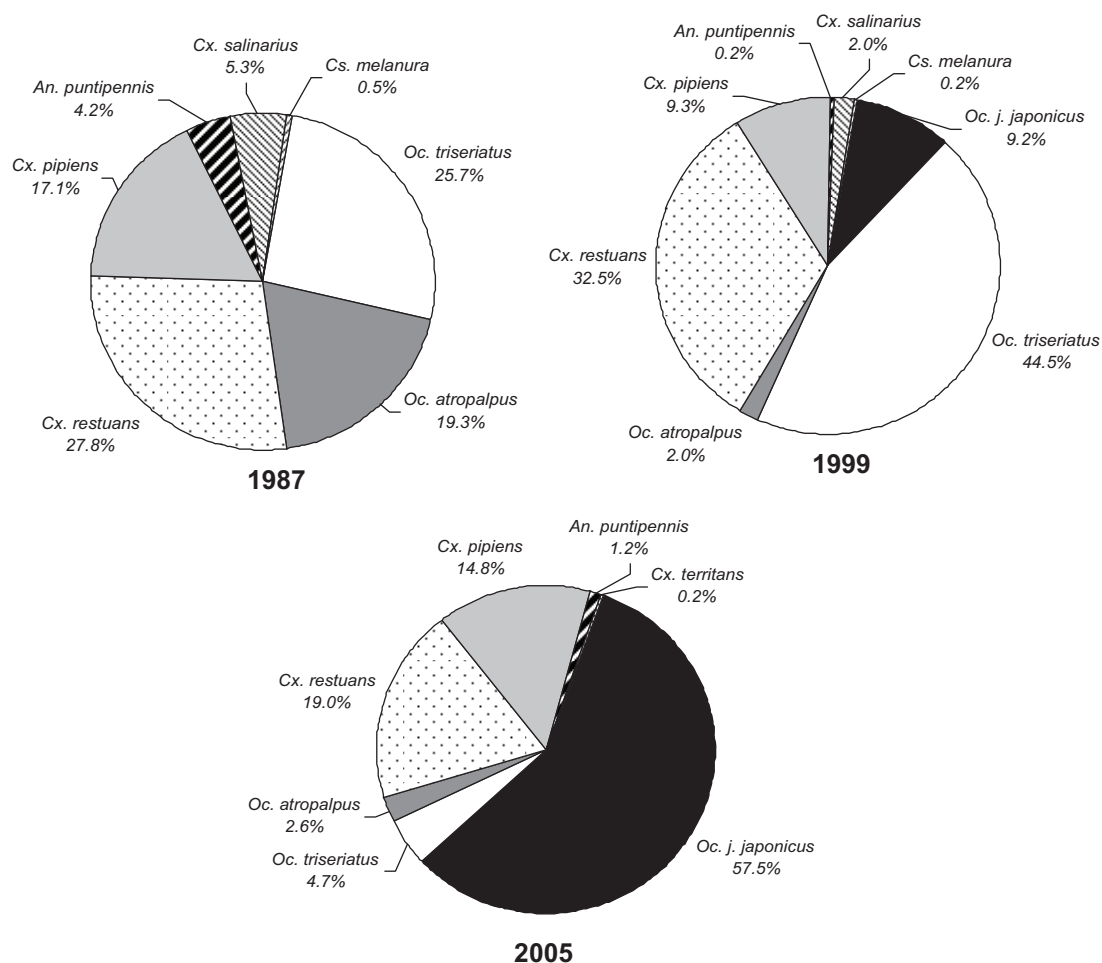
Fig. 3. Comparative relative abundance of mosquito species collected from waste tire disposal sites from June through October of 1987 ($n = 935$), 1999 ($n = 2,347$), and 2005 ($n = 5,415$).

River in Kent in 2005, with that obtained from a prior survey at this site during the same time period (July through November) in 1999 (Fig. 5; Table 3), revealed a significantly greater proportion of *Oc. j. japonicus* in 2005 ($n = 8,047$) in comparison to 1999 ($n = 3,975$) (68.8% versus 56.0%, $\chi^2 = 188.7$, df $= 1$, $P < 0.001$). This was concomitant with significant declines in the pro-

Table 2. Estimated avg no. of mosquito larvae collected per tire from waste tire disposal sites in Connecticut from June to Oct. of 1987, 1999, and 2005

Mosquito species	1987	1999	2005
Oc. atropalpus	0.16	0.04	0.02
Oc. j. japonicus	—	0.18	0.53
Oc. triseriatus	0.21	0.87	0.04
Cx. pipiens	0.14	0.18	0.14
Cx. restuans	0.23	0.63	0.18
Cx. salinarius	0.04	0.04	—
Cx. territans	—	—	0.02
Cs. melanura	0.004	—	—
An. punctipennis	0.03	0.004	0.01

portional abundance of *Oc. atropalpus* (14.6 versus 17.7%, $\chi^2 = 19.5$, df $= 1$, $P < 0.001$) and *Cx. restuans* (7.9 versus 24.7%, $\chi^2 = 641.8$, df $= 1$, $P < 0.001$). Although representing a relatively smaller percentage of the total mosquitoes collected, all three minor species ($<5\%$ each) were significantly more prevalent in 2005 than in 1999: *An. punctipennis* (4.3 versus 0.6%, $\chi^2 = 123.1$, df $= 1$, $P < 0.001$), *Cx. territans* (2.5 versus 0.2%, $\chi^2 = 82.3$, df $= 1$, $P < 0.001$), and *Cx. pipiens* (1.9 versus 0.8%, $\chi^2 = 19.0$, df $= 1$, $P < 0.001$).

Discussion

With this investigation we have documented increased relative abundance of larval populations of *Oc. j. japonicus* in natural rock pool and discarded tire habitats associated with significant declines in the relative abundance of several resident native species including *Oc. atropalpus*, *Oc. triseriatus*, and *Cx. restuans.* Among the 13 waste tire disposal sites sampled throughout the state, *Oc. j. japonicus* was the predom-
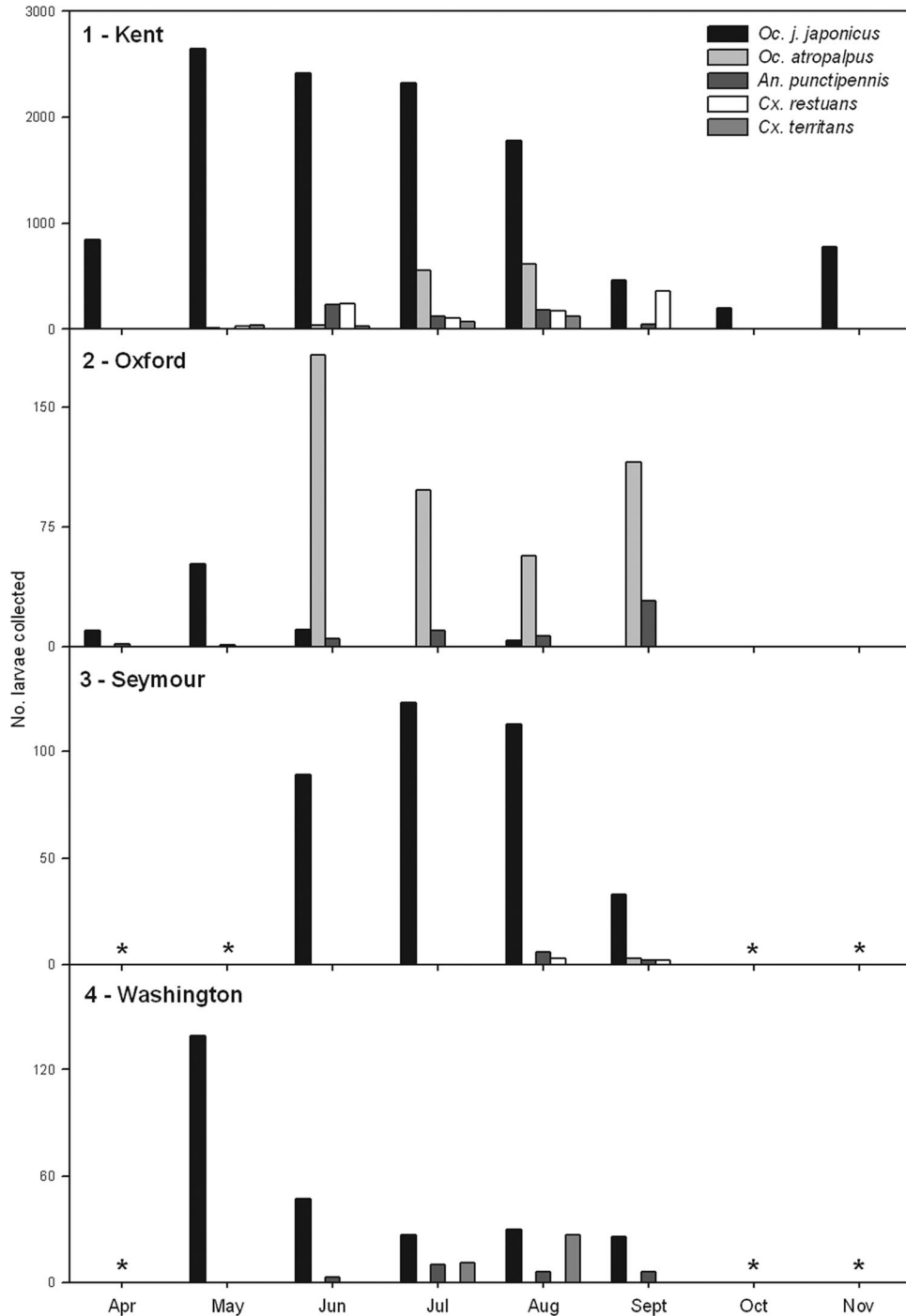
Fig. 4. Total monthly number of *Oc. j. japonicus, Oc. atropalpus, An. punctipennis, Cx. restuans,* and *Cx. territans* larvae collected from four rock pools sites sampled from April to November 2005. *, not sampled.

inant species regardless of surrounding landscape features (urban or forested), accounting for nearly 56% of all larvae collected. This mosquito was also the most abundant species found each month, with the exception of April and November when populations of all species were comparatively small. A comparison with collections from a prior statewide survey of used tire piles made in 1999, when *Oc. j. japonicus* was first detected, revealed a 90% reduction in the relative abundance of larval populations of *Oc. triseriatus,*
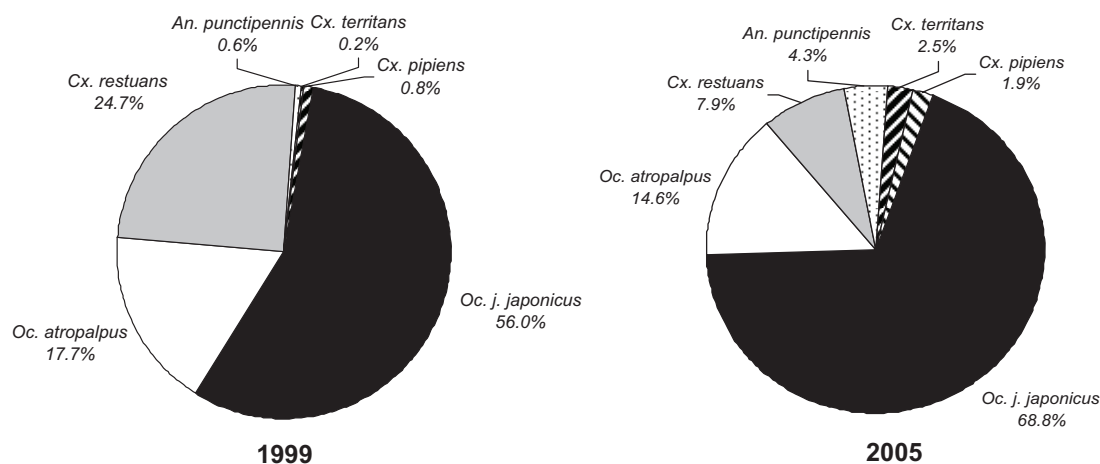
Fig. 5. Comparative relative abundance of mosquito species collected from rock pools in Kent, Connecticut from July to November of 1999 ($n = 3,975$) and 2005 ($n = 8,047$).

which was the predominant species encountered at the time. An equally marked reduction was also apparent among larval populations of *Oc. atropalpus*, which comprised a significantly greater proportion (19.3%) of the larval mosquito population inhabiting used tire piles in 1987, before the detection and presumed introduction of *Oc. j. japonicus* into the state (Andreadis et al. 2001). The reduced prevalence of *Oc. atropalpus*, first noted in 1999, appears to have remained virtually unchanged through 2005, where it coexists, but now accounts for only 2.0% of all species. A significant reduction in the proportional abundance of another native species, *Cx. restuans* was also apparent, but it was not nearly as pronounced. Among the major species inhabiting used tire casings, only *Cx. pipiens*, itself a non-native invasive species, appeared to be unaffected by the expansion of *Oc. j. japonicus*, retaining abundance levels that were comparable to those observed before invasion.

Our detection of an increased abundance of *Oc. j. japonicus* in used tire habitats throughout the state of Connecticut coincident with declines in the prevalence of *Oc. triseriatus* and *Oc. atropalpus*, concurs with a parallel shift in species composition recently noted among mosquitoes inhabiting abandoned tire piles in West Virginia (Joy et al. 2003, Joy 2004, Joy and Sullivan 2005), where *Oc. j. japonicus* was reported to have supplanted *Oc. triseriatus* as the dominant species in the state while populations of *Oc. atropalpus* were comparatively rare. Joy and Sullivan (2005) further concluded that *Oc. j. japonicus* was a significantly better colonizer of tires than *Oc. triseriatus* in peridomestic, sunlit conditions throughout West Virginia whereas both species were equally likely to colonize tires in nonperidomestic, shaded settings. This led the authors to suggest that *Oc. j. japonicus*, with its more catholic use of tire habitats and temporal dominance had the potential to displace *Oc. triseriatus* in used tire habitats. Although no attempt was made in the current investigation to evaluate the comparative abundance of *Oc. j. japonicus* in tires exposed to direct sunlight with those shaded by low-lying vegetation, our documentation of an increased prevalence of *Oc. j. japonicus* in tire casing located in a wide variety of environments support this view. The potential for *Oc. j. japonicus* to displace larval populations of *Oc. triseriatus* in used tire casings has been further documented in a study by Burger and Davis (2008), who monitored larval abundance of these two species in 12 used tire casings that were placed inside the edge of a mixed oak, maple, and white pine woodland forest in southeastern New Hampshire over a 5-yr period. During that period, the authors recorded increasing abundance of *Oc. j. japonicus* from 18 to 81% coincident with a virtually identical decline in the abundance of *Oc. triseriatus* from 82 to 19%. Our findings are also in agreement with a survey of mosquitoes inhabiting "bunker tires" on dairy farms in neighboring southeastern New York (Dutchess County) (Kaufman et al. 2005), where *Oc. j. japonicus* was similarly found to be the predominant larval mosquito species, accounting for 42% of recovered specimens. Also noted in that study was a modest increase in the number of *Oc. j. japonicus* collected from tires on dairy farms in the central region of the state from <1% in 2001 to 5% in 2002, leading the authors to suggest that *Oc. j. japonicus* might be competitively excluding local tire-breeding species such as *Cx. pipiens* and *Cx. restuans* in some

Table 3.   Average no. of mosquito larvae collected per rock hole from the Housatonic River in Kent, Connecticut from July to Nov. of 1999 and 2005

Mosquito species	1999	2005
Oc. atropalpus	4.26	4.11
Oc. j. japonicus	13.49	19.41
Cx. pipiens	0.21	0.54
Cx. restuans	5.95	2.23
Cx. territans	0.05	0.72
An. punctipennis	0.14	1.22

regions of the state. We found no evidence for competitive exclusion of either *Culex* species in used tire habitats in Connecticut, as both species appear to effectively coexist, collectively accounting for one-third of all species. However, we did observe a significant decline in the relative abundance of *Cx. restuans* from prior surveys.

Our observations on the abundance of *Oc. j. japonicus* in rock pools along stream beds were consistent with the propensity of this species to favor these highly specialized habitats in its native range in Japan and Korea (Tanaka et al. 1979). With one notable exception, *Oc. j. japonicus* was the most abundant mosquito collected throughout the season (April to November) in these watershed locations, accounting for nearly 80% of all collected larvae. Our demonstration of increased abundance of *Oc. j. japonicus* in conjunction with declines in the relative proportion of native populations of *Oc. atropalpus* and *Cx. restuans* from the same rock pools sampled in Kent 6 yr earlier, further support our conclusion that this invasive mosquito is expanding its range in this preferred microhabitat. This conclusion is consistent with a recently completed survey of rock pool habitats in heavily forested mountainous regions of the southern Appalachians (North Carolina, South Carolina, Georgia), where Bevins (2007) detected a large preponderance of *Oc. j. japonicus* in rock pools associated with all major rivers in the region and 83.3% of all sites sampled, while larval populations of *Oc. atropalpus* were notably less abundant occurring in only 16.6% of the rock pools. Scott et al. (2001) similarly reported an abundance of *Oc. j. japonicus* larvae from a series of natural rock pools along the Delaware Water Gap in New Jersey, representing 46.7% of all larvae collected in June and July, and a complete absence of *Oc. atropalpus* larvae despite its broad historical distribution throughout the state.

The only rock pools where *Oc. j. japonicus* did not predominate in the current study were those located in Oxford, where water temperatures were notably warmer and exceeded 30°C from June through September. These pools were dominated by *Oc. atropalpus*, a species that is known to exhibit a proclivity for colonizing open sunlit areas (Beier et al. 1983, Berry and Craig 1984, Andreadis 1988, Lampman et al. 1997, Joy et al. 2003). The near exclusion of *Oc. j. japonicus* from warm water pools fully exposed to the sun is significant and suggests that a temperature barrier may exist for this species and that populations may not be able to effectively colonize regions of the United States with relatively high summer temperatures. This hypothesis conforms to the southernmost distribution of *Oc. j. japonicus* in the Kyushu region of Japan (32°N latitude) (Tanaka et al. 1979) and the most current southern distribution record of this species in the continental United States, Fulton County, GA (33°68′N latitude) (Gray et al. 2005). It is also noteworthy that despite the detection of a single adult female from a gravid trap in the extreme northeastern corner of the state of Alabama in June 2005 (Mullen 2005), no *Oc. j. japonicus* larvae were found in a concurrent state-wide survey of 169 tire sites from all 67 Alabama counties in 2004 and 2005 (Qualls and Mullen 2006).

Although it was not possible in this field study to directly examine the ecological processes and mechanisms responsible for this shift in relative abundance, the observations reported herein and elsewhere support the view that *Oc. j. japonicus* is an effective competitor in rock pool and tire environments and may be responsible for reducing populations of several native species occupying these habitats through interspecific competition for limited resources. Interspecific competition and interference competition, wherein one species inhibits the growth and development of another, are among the most common mechanisms affecting species displacement and reduction where resources are limited such as tires or rock pools, and are characteristics of successful invasive species that are most often revealed through initial decline or elimination of ecologically similar species that inhabit the same community as observed in this investigation (Juliano 1998, Juliano and Lounibos 2005, Lounibos 2007). According to Juliano and Lounibos (2005), interspecific competition "encompasses any mechanism that produces negative effects on population growth of the focal species, including resource competition (via depletion of shared resources), chemical or physical interference (via toxins, waste products, or aggression), and mating interference (via interspecific mating depressing reproductive output)." Interspecific larval competition has also been proposed as one of the more likely mechanisms responsible for the invasion success of other invasive and non-native mosquitoes throughout various regions of the globe including *Ae. aegypti* (L.), *Ae. albopictus* (Skuse), *Cx. pipiens* (L.), *Cx. quinquefasciatus* (Say), *An. gambiae* (Giles), and *Oc. bahamensis* (Berlin) (=*Ae. bahamensis*, see Reinert 2000) (Juliano 1998, Juliano and Lounibos 2005, Lounibos 2007).

In addition to interspecific resource competition, it is important to acknowledge that other factors may potentially impact interactions among *Oc. j. japonicus* and other resident species, and help to explain the larval community structure observed in used tire and rock pool habitats. These factors have been reviewed by Juliano and Lounibos (2005) and include: apparent competition caused by shared parasites that have asymmetrical negative effects on their respective hosts (Juliano 1998), intraguild predation wherein late instar larvae of one species are facultatively predaceous on smaller larvae of another species (Edgerly et al. 1999), differential vulnerability to predation (Grill and Juliano 1996, Griswold and Lounibos 2005) and tolerance to parasites (Aliabadi and Juliano 2002).

Larval competition between *Oc. j. japonicus* and *Oc. atropalpus* in simulated rock pools was recently evaluated by Armistead et al. (2008) who showed that the performance of both species was more significantly impacted by intraspecific conditions than by interspecific conditions at the same mosquito density. *Oc. atropalpus* appeared to be more sensitive to larval densities than *Oc. j. japonicus* because it requires a lengthened period of larval development to obtain

nutrient reserves for autogenous egg development. The authors concluded that this requirement may put *Oc. atropalpus* at a disadvantage under conditions of competition and limited resources, thus conferring a slight competitive advantage for *Oc. j. japonicus*. However, they also noted that the excessively stressful experimental conditions may have obscured the effects of larval competition between the two species.

Clearly there is a need to further investigate mechanisms affecting populations of *Oc. j. japonicus* and native resident species that appear to be in decline in rock hole and used tire microhabitats under ecologically realistic conditions. Efforts should additionally be made to examine mosquito community structure in tree-hole habitats in forested areas where *Oc. triseriatus* may have a competitive advantage and for which we have no current information. Lastly, continued monitoring of larval mosquito populations is these specialized habitats would also appear to be warranted in an attempt to further elucidate how communities change over time and space.

Acknowledgments

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